THE DISTRIBUTION AND REPRODUCTION OF SAGITTA ELEGANS ON GEORGES BANK IN RELATION TO THE HYDROGRAPHICAL CONDITIONS

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During the past few years an investigation has been undertaken of the factors underlying the productivity of Georges Bank, an extensive fishing area lying east of Cape Cod (Fig. 1). The economy of this area depends upon various interdependencies of the fish populations, the bottom fauna, and the plankton; and all are profoundly affected by the complex of strong currents and persistent eddies which are found on the Bank. In order to understand the essential ecological relationships, it is therefore necessary to gain a knowledge of both the hydrography and the biology of the waters of the region.

The present study of the abundance, distribution, and seasonal cycle of reproduction of the chaetognath, *Sagitta elegans*, was undertaken first because this species forms a prominent element in the zooplankton of Georges Bank, and second because Sagitta may be used as a "current indicator" to aid in unravelling the involved current system of the region. This species is a relatively large, easily recognized member of the zooplankton and its body length and maturity stage are readily determined. The life span of *Sagitta elegans* is sufficient to bridge periods of six weeks or more, with the result that in cases where observations are repeated each month, the same population may be identified from one cruise to the next. This condition presents a desirable contrast to more rapidly reproducing organisms, such as diatoms, in which populations of large dimensions may appear or disappear within a week or so.

Certain relatively recent investigations of the ecology of Sagitta in other regions are available for comparison, but none had the advantage of our quantitative collection method, nor the opportunity for revisiting as frequently over a two-year period an extensive net-work of stations as characterized the present undertaking. The breeding and growth of *Sagitta elegans* was studied by Russell (1932; 1933) off Plymouth, England, and by Pierce (1941) in parts of the Irish Sea. *Sagitta elegans* has been employed successfully as a current indicator in British waters by Russell (1939) and the distribution of the species by currents in the Gulf of Maine has been critically investigated by Redfield and Beale (1940).

Collection and Analysis of Material

Samples of plankton and hydrographic data for the present study were obtained from the research vessel, "Atlantis", during eleven cruises to Georges Bank from September 1939 to June 1941 (Table I). On each cruise a net-work of 21 to 52 stations was occupied over the Bank. In all cruises (except that of

[1] Contribution No. 328.

January, 1940) the stations were ordinarily placed at 15-mile intervals on five or six parallel sections, about 25 miles apart, running SE and NW across the Bank and into the immediately adjacent waters. The location of the stations is indicated in the charts showing the distribution of Sagitta (Figs. 5 and 6). The stations covered the region from South Channel on the southwest to the eastern tip of Georges Bank and from the deep basin of the Gulf of Maine on the northwest to the edge of the continental shelf on the southeast. No stations

Table I

List of cruises to Georges Bank

Cruise no.	Date	No. of stations	Station serial nos.
89	Sept. 6–13, 1939	52	3629–3680
93	Jan. 4–11, 1940	21	3726–3746
95	Mar. 21–Apr. 2, 1940	35	3792–3826
96	Apr. 17–27, 1940	26	3827–3852
97	May 9–16, 1940	33	3856–3888
98	June 1–8, 1940	36	3892–3927
100	June 19–27, 1940	36	3932–3967
112	Mar. 21–Apr. 2, 1941	33	4177–4209
113	Apr. 15–23, 1941	34	4210–4243
114	May 7–14, 1941	34	4244–4277
116	May 28–June 4, 1941	33	4278–4311

could be made in the immediate vicinity of Cultivator and Georges Shoals. The segment of the ocean covered by the station net-work of each cruise was more than 150 miles long and 100 miles wide, or an area larger than the states of Massachusetts, Connecticut, and Rhode Island combined (Fig. 1).

Standard hydrographic observations for salinity and temperature were made at every station and Secchi disc measurements of transparency were carried out during daylight stations. Studies of certain chemical characteristics of the water and of the phytoplankton population were undertaken by collaborating investigators (Sears, 1941; and Riley, 1941 and 1942).

The zooplankton was collected at each station by means of two or more hauls with Plankton Samplers (Clarke and Bumpus, 1940) and one haul with a stramin net. Sagittae were taken in adequate numbers in both types of equipment and the two sets of hauls served as a check on one another.

The opening of the Plankton Sampler, which is 12.7 cm. in diameter, is provided with a shutter, and each instrument contains a meter which records the amount of water filtered by the net. In the present case, the instruments were equipped with No. 2 silk nets (22 strands/cm.) and "oblique" hauls [1] were made at a speed of about 2 knots for periods of 25 to 40 minutes. Ordinarily between 10 and 20 cubic meters of water were filtered during each tow, but the action of

[1] In an "oblique" haul the net is towed horizontally but is raised in steps so that the whole depth of the stratum concerned is sampled. The Sampler could be towed safely down to within three meters of the actual bottom.

the tide or of clogging was such that values as low as 5 m.^{3} and higher than 30 m.^{3} were recorded. This variation makes clear the need for measuring the amount of water which actually passes through the net. The Samplers were arranged vertically so as to divide the total depth of water into two or three strata and, when feasible, were attached to the same cable. The uppermost

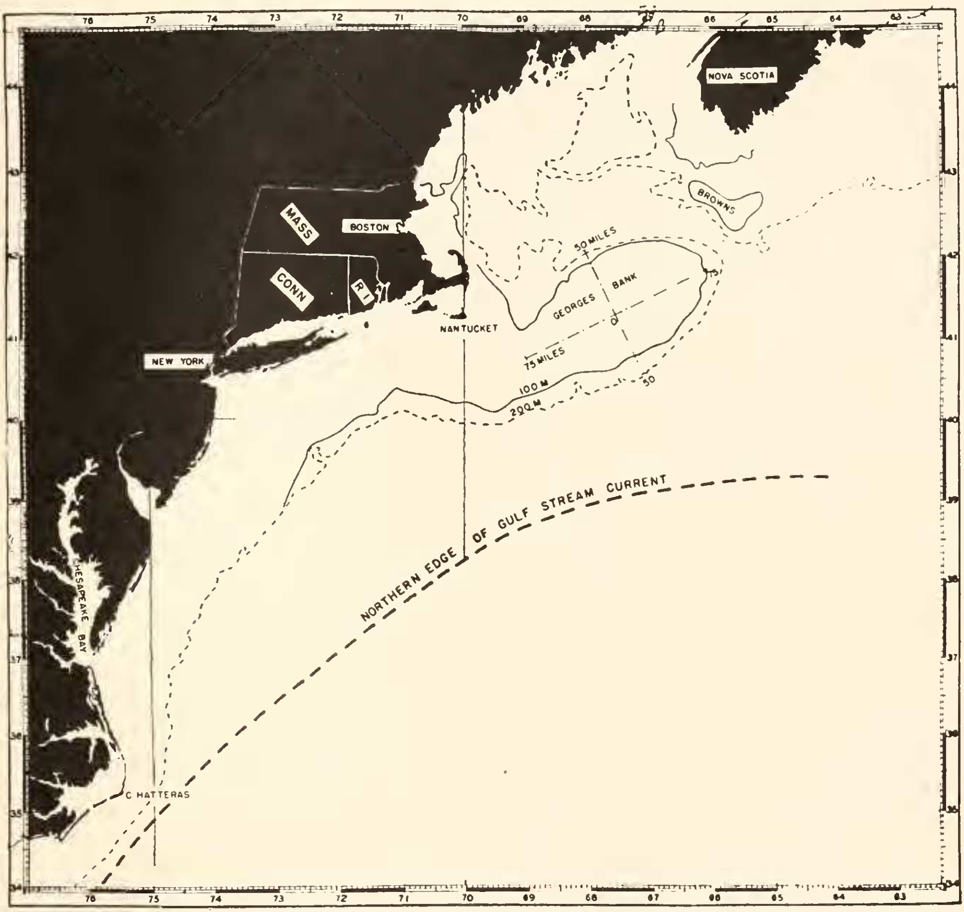

FIGURE 1. Orientation map of Atlantic Coast. The location and relative size of Georges Bank are indicated.

instrument sampled the "Shallow" Stratum, extending from a depth of 25 m. to the surface. The lower limit of this stratum corresponded roughly with the position of the thermocline in those areas where it existed. At stations where the water was less than 75 m. deep, the "Second-depth" Stratum extended from the bottom to 25 m. In water deeper than 75 m., however, the remaining distance to the bottom (or to a maximum depth of 200 m.) was divided into two equal parts and these comprised the "Second-depth" and the "Deep" Strata respectively. The vertical distribution of the sagittae could therefore be studied on the basis of these strata:

Stratum	Water less than 75 m.	Water more than 75 m.
"Shallow"	0 m. to 25 m.	0 m. to 25 m.
"Second-depth"	25 m. to bottom	25 m. to half distance to bottom (or to half distance to 200 m.)
"Deep"	——	Remaining distance to bottom (or to 200 m.)

The stramin net (Diameter: 1.5 m., Mesh: 6 strands/cm.) was equipped with rollers at the lower edge of its frame in order that it could be safely lowered until it touched the bottom. One "oblique" haul was made from the bottom (or from a depth of 200 m.) to the surface at each station. When proper allowance

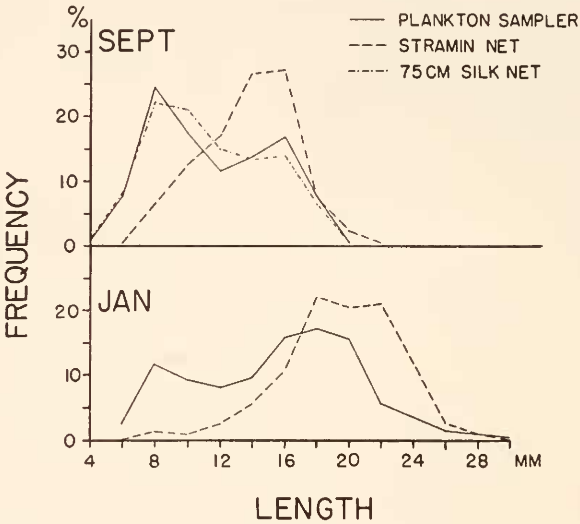

FIGURE 2. Comparison of length frequency distribution of *Sagitta elegans* for the following types of nets:

Plankton Sampler (12.7 cm. in diameter) with No. 2 silk.
Silk net (75 cm. in diameter) with No. 2 Silk.
Stramin net (1.5 m. in diameter).

was made for the difference in the sizes of the apertures of the stramin net and the Plankton Samplers, a good agreement was found between the numbers of sagittae taken by the former and the sum of the catches of the latter at each station.

Before the work was begun, it was doubted whether the relatively small Plankton Sampler would catch the larger sizes of an active animal, such as Sagitta, in their true proportions. For the first cruise (September 1939), therefore, a silk net 75 cm. in diameter and of the same mesh, was towed immediately below the Plankton Sampler. Since comparison of the length frequency distribution of the sagittae taken by the two sizes of nets showed exceptionally good agreement (Fig. 2), it is felt that the catch of the Plankton Sampler can be relied upon. In the January cruise sagittae as large as 30 mm. in length were retained by the Sampler. On the other hand, the stramin net was shown not to retain adequately the smallest sizes of sagittae. For these reasons and especially because of the accuracy of the determinations of depth and volume with the Plankton Samplers, the ensuing analysis of the abundance and distribution of the Sagitta populations is based primarily upon the hauls with these instruments. The present observations can therefore be placed on a quantitative basis not hitherto possible.

The sagittae were separated from the remaining plankton in the laboratory and the species present were identified and enumerated.[1] The great majority of sagittae were *Sagitta elegans* but specimens of *S. serratodentata* and a smaller number of *S. enflata* were encountered in certain hauls from the periphery of Georges Bank. For each station the average number of *S. elegans per cubic meter* was calculated *for each stratum* by dividing the number caught in each haul by the volume of water filtered by the Plankton Sampler. The total number of individuals *under each square meter* of sea surface was found by multiplying the number per cubic meter for each stratum by the thickness of the appropriate stratum and then adding these products together. Finally the *average number of animals per cubic meter for the whole water column* at each station was obtained by dividing the foregoing value by the total depth of water at each station. These average values per cubic meter (or per ten cubic meters) have been plotted on the charts showing quantitative distribution (Figs. 5, 6, and 10), but they may readily be re-converted to the "per square meter" basis by multiplying by the depth in each case.

Length measurements were made of all specimens of *Sagitta elegans* in each haul up to a maximum of 50. The stage of maturity was also determined for the individuals of this species in most of the hauls in each cruise from all parts of the Bank. Animals from each haul (usually between 20 and 50 individuals) were stained by the method described by Pierce (1941, p. 115), and then were classified as Stage I—*Immature*, Stage II—*Intermediate*, or Stage III—*Mature*, following the criteria of Russell (1932, p. 134).

General Hydrographical Conditions

The depth of the major portion of Georges Bank lies between 40 m. and 100 m., although areas of less than 25 m. occur in the north central portion, and the Shoals themselves are covered by only 5 to 15 m. of water. Along the northern edge of the Bank the bottom drops rapidly from about 40 m. to more than 200 m. as the deep basin of the Gulf of Maine is approached. Along the southern edge the depth changes somewhat more gradually from 100 m. to 200 m. Beyond 200 m. it increases rapidly to about 2000 m.

Georges Bank is therefore, roughly speaking, a submerged, flat-topped plateau (Fig. 3), and it presents a sufficiently large obstacle to water movement to produce a profound effect on the ocean currents of this region. Although the details of the water movements over and around the Bank have never been adequately determined, especially for the colder part of the year, it has been well established in general that during the summer months at least, water from the Gulf of Maine

[1] The authors are indebted to Miss Dorcas Delabarre for technical assistance in the analysis of the Sagitta material.

does not flow directly across the Bank but tends to move around the eastern and southern margins of the Bank in a clockwise direction, leaving a relatively stationary eddy of water over the central part of the Bank. From the point of view of the ecology of the Bank, our interest in the current system lies in the question of the degree of permanence of this eddy, and in the extent to which the "bank water" can be regarded as biologically isolated from the surrounding regions.

The eddy on the Bank might be dislodged by relatively slight changes in the strength or position of the surrounding ocean currents (Iselin, 1939), or it might be disrupted by the action of certain local agents. The strong tidal currents on

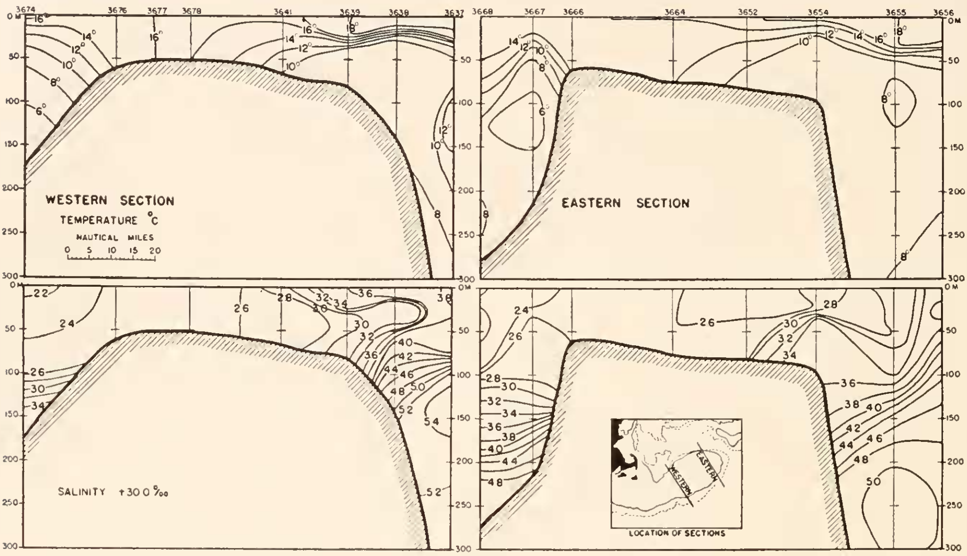

FIGURE 3. Vertical sections for temperature and salinity for September 1939 (cruise 89). The contour of Georges Bank is indicated by the cross hatching from the Gulf of Maine on the left to the edge of the Continental Shelf on the right. Station numbers appear at the top of the diagrams. The figures on the salinity curves are to be increased by 30 to give the actual values in parts per mille.

the Bank cause the overlying water to oscillate in generally elliptical paths, the long diameters of which may exceed eight miles. Winds, which frequently reach gale velocities, sweep unimpeded across the area, tending to force the surface water along with them. The danger would thus appear to exist that from time to time the bank water might be swept entirely off the Bank, carrying with it the pelagic stages of animals which, as adults, could live only in a bank environment, or removing an element of the plankton which is essential to the economy of the Bank. Even though no cataclysmic dislocation of the bank water occurred, it is important to know to what extent a dilution or a renewal of the water mass may take place through continuous or intermittent admixtures of new water from one direction or another.

The turbulence produced by the tidal currents and by the wind in the relatively shallow water overlying Georges Bank causes a vertical mixing of the water which results in a nearly uniform distribution of temperature and salinity from top to bottom at all seasons of the year, particularly in the central part of the Bank. The bank water thus contrasts sharply with the surrounding water masses, which are typically stratified during all except the winter months. Since the temperatures and salinity values on the Bank are generally intermediate between those of the surface and the deeper strata on the Gulf of Maine but usually much lower than those of the water lying to the south, we know that the bank water is originally derived, in a large part at least, from the Gulf (Figs. 3 and 4). That portion of the Bank over which vertically uniform water was found is termed the *Mixed Area*, and all stations at which the salinity does not vary by more than 0.2 part per mille from surface to bottom are considered to

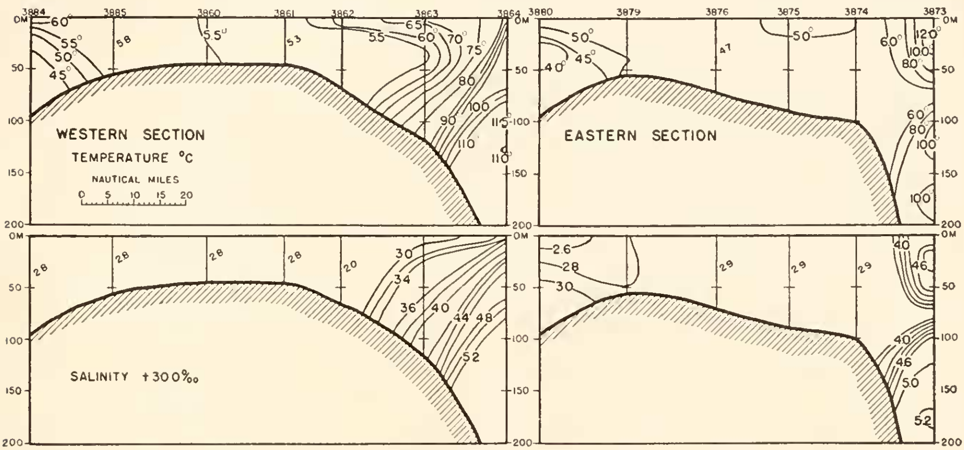

FIGURE 4. Vertical sections for temperature and salinity for May 1940 (cruise 97).

lie within it.[1] The limits of the Mixed Area are ordinarily rather sharp, and have been indicated by a heavy broken line in the charts of Sagitta distribution for each cruise (Figs. 5, 6, and 10).

The vertical uniformity of the temperature and salinity within the Mixed Area presents an ecological condition for the Bank organisms which is quite unlike that for the oceanic forms living in the stratified water of the adjacent deeper areas. Moreover, seasonal changes in these factors are somewhat damped by the continued vertical mixing, as is seen by reference to Tables II and III. The seasonal range in temperature for the Mixed Area extended from a minimum of about 2.5° C. to a maximum of over 16° C. Surface temperatures in the regions to the north and to the south of Georges Bank were generally higher in summer and lower in winter. Furthermore, during the winter pelagic animals living at the surface in these neighboring areas could find warmer water by descending to lower strata, and similarly during the summer they could escape excessively high temperatures by seeking greater depths. In contrast, the fauna

[1] Uniformity of salinity, rather than temperature, was taken as the criterion for the Mixed Area because in the present situation salinity is less easily modified after the water has reached the Bank.

TABLE II

Comparison of temperatures in the Mixed Area and in the Stratified Water at the margins of Georges Bank

Values given are for typical stations near the center of the Bank and in the deeper water to the north and to the south. At the stations in the Mixed Area temperatures did not vary by more than 1.6° C. from surface to bottom and in most cases the variation was much less.

Date	Mixed Area	North Margin		South Margin	
	Aver. temp.	Surface	100 m.	Surface	100 m.
Sept., 1939	16.3° C.	16.4° C.	6.3° C.	19.3° C.	9.3° C.*
Jan., 1940	4.1	3.3	6.8	4.6	6.2*
Mar., 1940	2.5	2.1	5.3	2.8	3.9*
Apr., 1940	3.7	3.5	3.4	4.7	11.2
May, 1940	4.8	5.3	4.1*	6.1	7.8*
June 1–8, 1940	7.2	10.4	3.0*	10.8	9.3
June 19–27, 1940	8.5	10.6	3.1	10.3	10.2
Mar., 1941	2.7	3.3	4.1	2.9	4.9
Apr., 1941	3.9	4.3	4.5	3.2	4.9
May, 1941	4.6	6.5	5.4	4.0	4.5
June, 1941	6.8	9.1	3.6	7.3	5.4

* Value at somewhat less than 100 m.

TABLE III

Comparison of salinities in the Mixed Area and in the Stratified Water at the margins of Georges Bank

Values given are for typical stations near the center of the Bank and in the deeper water to the north and to the south. At the stations in the Mixed Area salinities did not vary by more than 0.2‰ from surface to bottom.

Date	Mixed Area	North Margin		South Margin	
	Aver. salinity	Surface	100 m.	Surface	100 m.
Sept., 1939	32.5‰	32.1‰	32.5‰	33.4‰	33.8‰*
Jan., 1940	32.8	31.5	33.7	32.9	33.2*
Mar., 1940	32.8	32.4	33.2	32.7	33.0*
Apr., 1940	33.0	32.5	33.1	33.0	35.3
May, 1940	32.8	32.5	33.2*	32.7	34.1*
June 1–8, 1940	32.8	31.8	32.9*	33.1	33.5*
June 19–27, 1940	32.7	32.0	32.9	32.5	34.4
Mar., 1941	32.7	32.8	33.1	32.7	33.4
Apr., 1941	32.5	32.5	33.2	32.1	33.5
May, 1941	32.5	32.3	33.4	32.1	33.4
June, 1941	32.7	32.3	32.8	32.6	33.5

* Value at somewhat less than 100 m.

of the central bank waters could reach a materially different temperature only by migrating laterally entirely out of the Mixed Area. A similar situation obtains in regard to salinity, although there is little evidence that changes in salinity, *per se*, of the magnitude encountered in this region are of ecological importance. On the other hand, differences in density, which result in large part from the salinity, are bound to be critical for passively floating organisms, and the lack of a pronounced vertical density gradient in the Mixed Area, as well as the excessive turbulence there, presents a very special problem for such forms.

Quantitative Distribution of Sagitta Elegans

Vertical Distribution

The numerical abundance of *Sagitta elegans* varied greatly among individual hauls, ranging from a maximum of 165 specimens per cubic meter [1] to zero. When the hauls of each cruise are considered together, however, certain general trends in the changes in the Sagitta population become clear. The changes in horizontal distribution from cruise to cruise will be presented in the next section. In this section the variations in the vertical distribution will be considered as derived at each station from the separate hauls with the closing Plankton Samplers for the Shallow Stratum, the Second-depth Stratum, and the Deep Stratum. At stations where the depth of water was less than 75 m. the Second-depth haul extended to the bottom. Since this situation obtained at the majority of stations within the Mixed Area, the chief comparison for vertical distribution is between the Shallow Stratum and the Second-depth Stratum.

It is obvious that vertical distribution at stations made during the day (between the hours of sunrise and sunset) had to be distinguished from the situation at stations made during the night, since a diurnal migration of the animals was to be expected (Russell, 1933). Furthermore, if a vertical migration of the Sagitta tended to take place, very different conditions would be met with according to whether the station was in the Mixed Area or in the Stratified Area. If the animals encountered a thermocline, their movement might be stopped, or reversed (cf. Clarke, 1934). For the foregoing reasons the hauls upon which the analysis of the vertical distribution of *Sagitta elegans* is based, have been subdivided into those made at stations in the Mixed Area and those made at stations in the Stratified Area and have been further subdivided in each case into day and night hauls.

The *average* abundance of *Sagitta elegans* for all stations in each of these categories varied considerably from cruise to cruise (Table IV). In September the larger number of animals was found in the Second-depth Stratum in all cases, although at night in the Mixed Area an almost equally great number was taken at the upper level. In the winter and early spring of 1940 much smaller average numbers of sagittae were encountered and the differences in the various strata were not large. A tendency for the largest hauls to occur in the Deep Stratum is to be noted for May 1940, but this generality does not hold for the more sizable catches of the June cruises of that year. During the early spring of 1941 small numbers of sagittae were again encountered and their vertical distri-

[1] Shallow stratum haul, May 30, 1941, made in south central part of Bank and consisting of very small individuals.

TABLE IV

Numerical abundance of S. elegans *in the separate strata. Average number per cubic meter in the indicated categories.*

X indicates an abundance of less than 0.1/m³. Values placed in parentheses are based on a total of less than 5 hauls.

Month	Cruise	Stratum	Mixed Area		Stratified Area	
			Day	Night	Day	Night
Sept., 1939	89	Shallow	5.3	17.5	0.7	1.6
		2nd Depth	10.8	17.9	8.1	(8.5)
Jan., 1940	93	Shallow	2.4	6.8	——	0
		2nd Depth	3.8	7.6	——	X
		Deep	(0.5)	(0)	——	0
Mar., 1940	95	Shallow	2.4	1.8	0	X
		2nd Depth	2.4	1.1	0	0.1
		Deep	(1.9)	(0.2)	X	X
Apr., 1940	96	Shallow	1.8	2.2	X	(0)
		2nd Depth	3.6	1.4	0.2	(0)
		Deep	(2.8)	——	(0.3)	(0)
May, 1940	97	Shallow	2.5	5.1	0.2	0.6
		2nd Depth	6.2	5.1	0.2	0.3
		Deep	(9.0)	(1.0)	16.6	13.0
June 1–8, 1940	98	Shallow	16.9	3.3	4.5	(3.3)
		2nd Depth	40.4	50.1	3.8	(5.9)
		Deep	(13.1)	(25.0)	3.6	(8.7)
June 19–27, 1940	100	Shallow	35.6	20.8	5.3	17.4
		2nd Depth	58.6	44.5	1.8	9.5
		Deep	——	(58.4)	3.4	12.6
Mar., 1941	112	Shallow	2.4	2.2	0	0.8
		2nd Depth	2.5	2.8	0	0.8
		Deep	(1.1)	(1.2)	X	1.2
Apr., 1941	113	Shallow	2.1	0.8	0	0.4
		2nd Depth	3.2	1.9	0	0.9
		Deep	(1.3)	(0.1)	0.1	0.1
May, 1941	114	Shallow	1.4	0.6	0	0.3
		2nd Depth	3.5	0.6	X	X
		Deep	(0.6)	(0)	0.3	1.0
June, 1941	116	Shallow	46.9	14.6	2.5	0.7
		2nd Depth	45.6	17.8	1.4	1.9
		Deep	(3.4)	(45.8)	1.6	2.5
Averages		Shallow	10.9	6.9	1.3	2.3
		2nd Depth	16.4	13.7	1.6	2.5
		Deep	3.7	14.6	2.9	3.9

bution was found to be generally uniform. This situation also held for May of that year, but in June much larger catches were made especially in the two upper strata for the day hauls and for the Deep Stratum for the night hauls in the Mixed Area.

In order to ascertain what tendency existed toward vertical diurnal migration it is not satisfactory to employ the foregoing average values because of the likelihood that a few large hauls would obscure differences occurring in stations with smaller representation. Accordingly a calculation has been made of the percentage of stations in each category for each cruise at which the number of *Sagitta elegans* in the Second-depth haul was greater than in the Shallow haul (Table V). When the data are scrutinized on this basis, it becomes clear that a

TABLE V

Comparative vertical distribution of S. elegans *for day and night hauls*

Percentage of Stations at which the number of animals per cubic meter in the "Second-Depth" haul was greater than in the "Shallow" haul. Values placed in parentheses are based on a total of less than 5 cases.

Month	Cruise	Mixed Area		Stratified Area	
		Day	Night	Day	Night
Sept., 1939	89	100%	29%	93%	50%
Jan., 1940	93	60	57		(100)
Mar., 1940	95	64	43		(67)
Apr., 1940	96	71	25	(100)	
May, 1940	97	86	50	60	(0)
June 1–8, 1940	98	70	71	(67)	(67)
June 19–27, 1940	100	75	100	20	33
Mar., 1941	112	78	70		(50)
Apr., 1941	113	73	(75)		(100)
May, 1941	114	75	(50)	(100)	(100)
June, 1941	116	46	80	(25)	50
Averages		73%	59%	66%	62%

definite vertical migration was taking place in both the Mixed Area and the Stratified Area at the time of the September cruise, since the majority of the animals were found below 25 m. in the day time and above 25 m. at night. A similar tendency, but less marked, was encountered in the first four cruises of 1940 and in the May cruise of 1941 for the Mixed Area. A reversal of the situation is to be noted for the June cruises in both 1940 and 1941, for in those cases the Second-depth hauls were greater at night at more stations than during the day. Taking the average for all cruises it is apparent that in all situations the deeper hauls were numerically greater in more than 50% of the cases. However, the variations encountered in vertical distribution and in diurnal migration from cruise to cruise show that the reactions of Sagitta in maintaining its vertical position in the water change materially according to the season or in relation to size and stage of maturity. A similar conclusion was reached by Russell (1933).

Horizontal Distribution Throughout the Year

The quantitative aspects of the distribution of *Sagitta elegans* will be examined in relation to the location of the water masses on Georges Bank for September

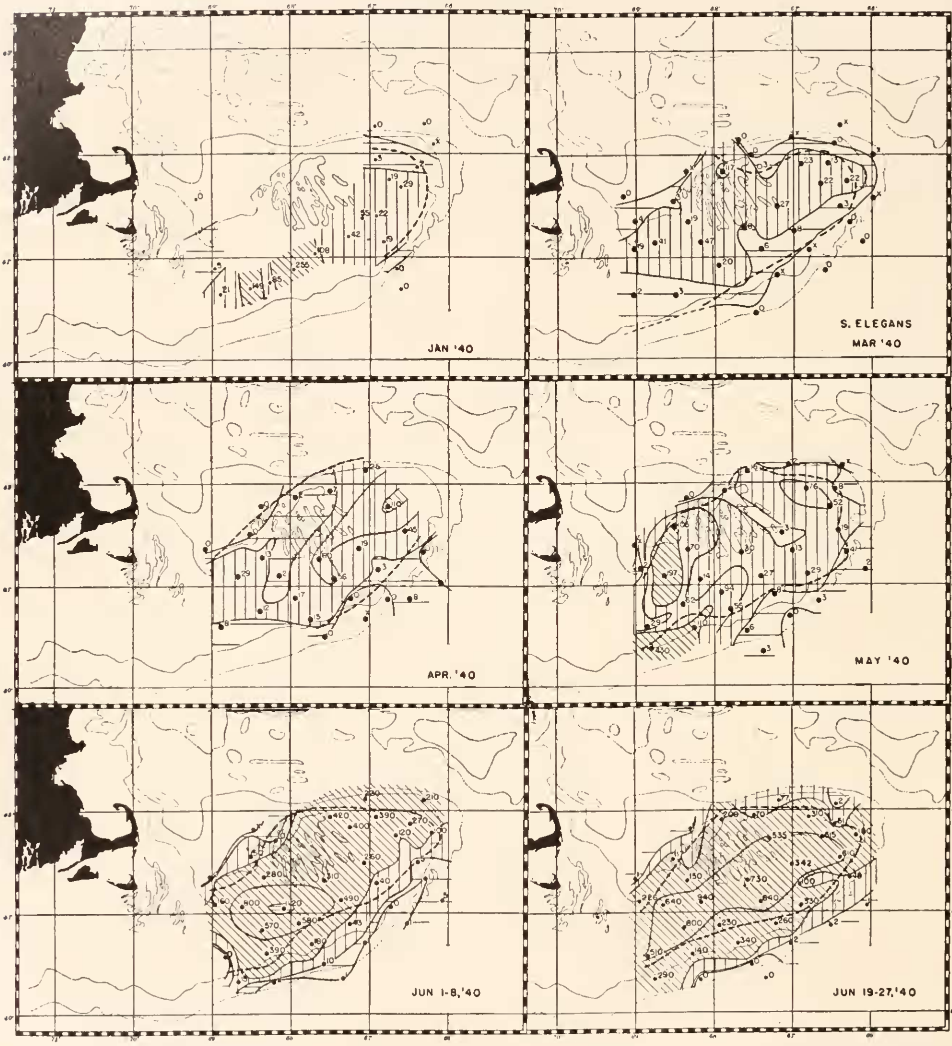

FIGURE 5. Distribution of *Sagitta elegans* on Georges Bank during 1940. January (cruise 93), March (cruise 95), April (cruise 96), May (cruise 97), June 1–8 (cruise 98), and June 19–27 (cruise 100). Average numbers per 10 cubic meters for whole water column for all stages. Plankton Sampler hauls. Boundary of Mixed Area indicated by heavy broken line.

1939 (Fig. 10), for the winter and spring of 1940 (Fig. 5), and for the spring of 1941 (Fig. 6). In each chart the station positions are designated by black dots and the *average* number of sagittae per 10 cubic meters *for the whole water column* at each station is indicated.[1] Contour lines representing concentrations of 1, 10, (50), 100, (500) and 1000 individuals per cubic meter have been drawn in. Progressively dense cross-hatching indicates areas of increasing numerical abundance. In addition, the position of the margin of the vertically homogeneous water of the Mixed Area for each cruise has been indicated by a heavy broken line superimposed independently on each chart.

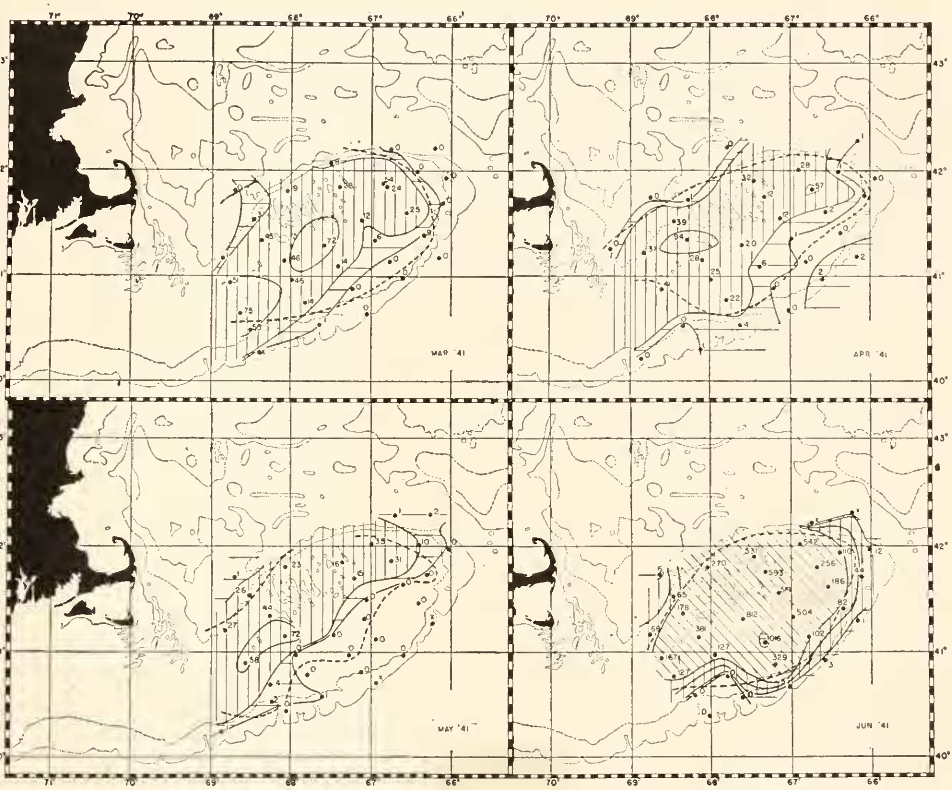

FIGURE 6. Distribution of *Sagitta elegans* on Georges Bank during 1941. March (cruise 112), April (cruise 113), May (cruise 114), and June (cruise 116). Average numbers per 10 cubic meters for whole water column for all stages. Plankton Sampler hauls. Boundary of Mixed Area indicated by heavy broken line.

Inspection of the chart for September 1939 (Figure 10, upper left) reveals the fact that at the time of this cruise extremely small numbers of *Sagitta elegans* occurred around the margins of the Bank (except possibly in the north central region). It is clear that the area of greatest concentration of this species lay in the center of the Bank. During this period the Mixed Area did not cover the whole of Georges Bank but was confined chiefly to the central portion except in the north where it extended beyond depths of 100 m. A rough correspondence

[1] The total number of sagittae *under each square meter* of sea surface may be derived from these values by multiplying by the depth (see "Collection and Analysis of Material").

is seen to exist for this cruise between the contour for 100 sagittae per 10 cubic meters (or 10 animals per cubic meter) and the limits of the Mixed Area.

A similar scrutiny of the distribution of *Sagitta elegans* may be undertaken for the succeeding cruises from Figures 5 and 6. A great variation in the numerical strength of this species during the year is indicated by the fact that although numbers greater than 10/m.[3] were encountered at nine stations in the September cruise, only one to four stations were as rich during the next four cruises. However, in each of the June cruises of 1940 about 20 stations yielded an average abundance of more than 10/m.[3] and one station of more than 100/m.[3] Similarly in 1941 during the first three cruises there were no hauls containing more than 10/m.[3] but in the June cruise this value was exceeded at 18 stations and there was one instance of an abundance greater than 100/m.[3] Although it was unfortunately not possible to make observations in every month of the year, as would have been desirable, the available information strongly indicates that the numerical strength of *Sagitta elegans* in the Georges Bank region reaches a low ebb in the winter and early spring, and attains high values beginning in June and perhaps extending through the summer.

In each of the eleven cruises the center of abundance of *Sagitta elegans* was found to be located within the central portion of the Bank and numbers dropped off toward the margin. Along the southern edge of the Bank the concentration of this species dwindled to a very small proportion and frequently to zero, especially beyond the 200 m. contour. Similarly low numbers were usually encountered along the eastern and northern margins although in some cruises an insufficient number of stations was occupied beyond the Bank to make certain of the limits of the population to the north. Since in most cases *Sagitta elegans* occurred in abundance at the westernmost stations of each cruise, we have definite indication that, at certain seasons of the year at least, numbers of this species are transported by westerly currents across South Channel toward Nantucket Shoals.

When the center of abundance of *Sagitta elegans* is compared with the location of the Mixed Area, it is clear that in spite of the changes in position of the latter from cruise to cruise, the greatest concentrations of the species were always found within the Mixed Area, and a close agreement existed between the contours of abundance and the boundary line of the mixed water (Figs. 5, 6, and 10). In addition to the situation in September, 1939, already described, striking cases of conformity between the distribution of the *S. elegans* population and the extent of the Mixed Area are seen in May and June (Fig. 6). During the May cruise stratified water was found to occupy the southern portion of the top of the Bank extending for 30 miles or more from the southern edge toward the center, whereas in June the mixed water largely covered this region. Corresponding to this shift in the position of the water masses *S. elegans* was found to be almost completely absent from the southern half of the Bank in May, but in June its distribution extended to the southern edge of the Bank.

In general the abundance of *S. elegans* tended to be relatively uniform for all the stations within the Mixed Area during each cruise. This fact showed that the spacing of the stations in this area was sufficiently close. The uniformity was no doubt due in large measure to the turbulence of the water in the Mixed Area and would not necessarily be expected in other regions of uniform hydrographic conditions but with less water movement.

Sagitta elegans is therefore chiefly abundant within the Mixed Area of Georges Bank, and during the periods covered by the present cruises, at least, this species appears to be largely isolated from surrounding regions. Evidence has been presented above that a small part of the population may be carried to the west at certain seasons by the movement of water around Nantucket Shoals. It is unfortunate that our observations could not have been extended to Cape Cod and to the waters north of the Cape in order to ascertain whether the sagittae of Georges Bank ever attain any important relationship with populations occurring in that region. As far as our present data go, however, no significant connection is indicated between the concentration of *S. elegans* in the vicinity of Massachusetts Bay reported by Redfield and Beale (1940) and the population on the Bank.

Growth and Breeding of Sagitta Elegans

Seasonal Changes in Length

The specimens of *Sagitta elegans* taken during the present investigation varied greatly in size, covering a range in length from 4 mm. to 30 mm. The frequency distribution of the sizes for all the hauls of the 1939–1940 cruises may be examined from the histograms of Figure 7. It is seen that no specimens longer than 20 mm. were taken in September, but individuals as long as 30 mm. occurred in January, March, and May. The modal length increased from 16 mm. in September to 18–20 mm. in January, and to 24 mm. in March. In April the modal length was 22 mm. These larger sizes were also represented in May and June, but in diminishing numbers.

Specimens of *Sagitta elegans* as small as 6 mm. were present in the September cruise in numbers nearly as great as the intermediate sizes. In January the presence of a secondary mode at 8 mm. suggests the simultaneous existence of two generations. In March and April, however, the smaller sizes were reduced to extremely small numbers and the intermediate sizes were poorly represented. Smaller individuals appeared in May and were more abundant in that month than the larger categories. By early June the numerical strength of this new crop of small Sagitta had increased ten fold and by late June they were still abundant. The modal length increased from 6 mm. in May to 8 mm. in June. Although in the late June cruise there were many more Sagitta in the 4 mm. class, an even greater augmentation of the sizes larger than 10 mm. was observed. Similar changes in the relative abundance and length distribution of this species were encountered during the cruises of 1941.

Scrutiny of the length distributions at the various individual stations and within the different strata revealed in general no tendencies for segregation. In most cases both large and small specimens were represented in the same relative proportions at the various depths at each station. Although considerable variation in length frequency occurred from station to station, nevertheless in most cruises there was no consistent tendency for large or small individuals to appear in certain parts of the Bank. An exception to the foregoing statement occurred in the cruise of May 1940, as shown in Figure 8, in which individual frequency distributions have been plotted for each station with sufficient numbers. In this case it is seen that at the easternmost stations only large specimens of

Sagitta elegans were taken, whereas at the western stations the smaller sizes definitely predominated. Evidently the remnant of the older animals persisted chiefly in central and eastern eddies, while the production of younger individuals was beginning most actively in the western parts of the Bank (see below).

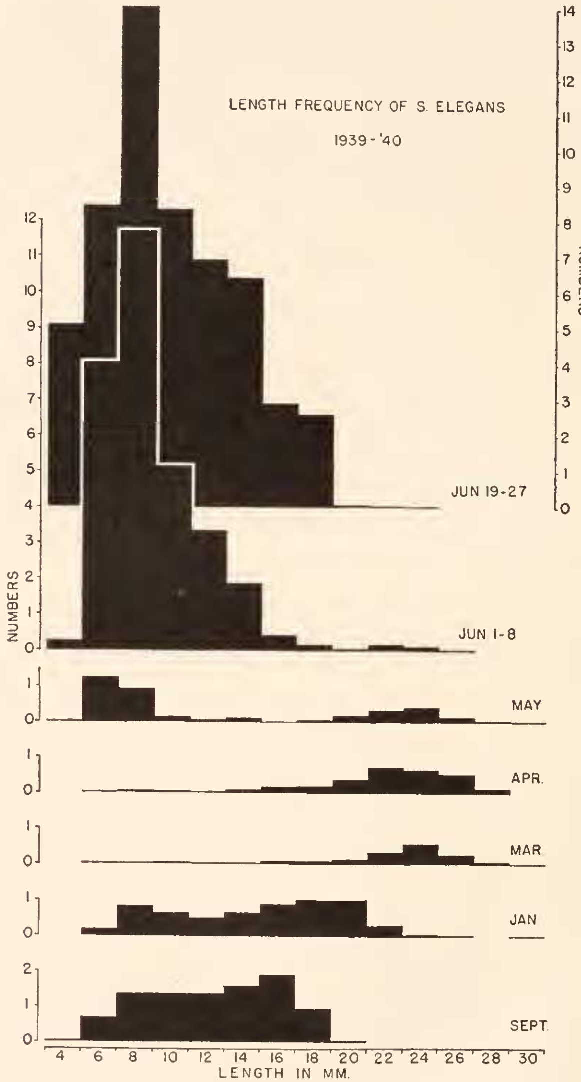

FIGURE 7. Average frequency distribution of lengths during 1939–40. Average numbers per cubic meter of *S. elegans* for each cruise.

Maturity Stages and Breeding Periods

Length measurements alone are not sufficient for determining the breeding periods of Sagitta because very great variations exist in the sizes of the three stages of maturity. This fact is amply demonstrated by the graphs of Figure 9, in which the length frequency distribution of each maturity stage has been plotted on a percentage basis for each cruise. Here it is seen that immature specimens (Stage I) may attain a length of 16 mm. or more, but individuals as short as 8 mm. may definitely have attained the "intermediate" condition (Stage II). Furthermore some specimens grew to lengths of 24 mm. or more while still in Stage II, while other individuals became completely mature (Stage III) at a length of 12 mm.

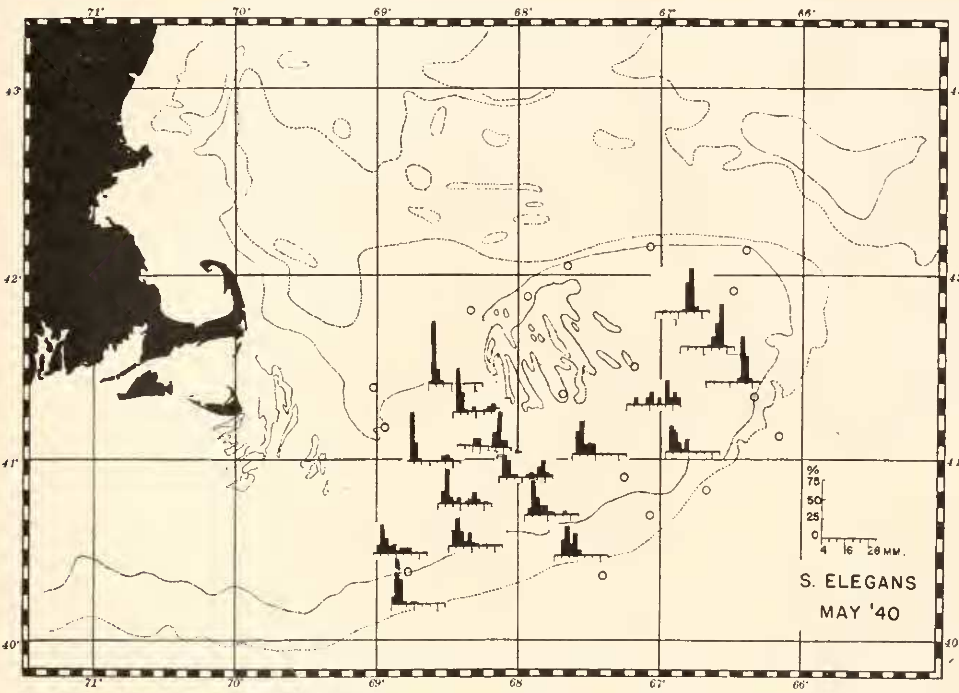

FIGURE 8. Length frequency distribution for individual stations in cruise of May 1940. Length measurements of *S. elegans* on percentage basis for individual stations, where numbers were sufficiently great.

From a study of the sequence of changes in the length and stage of maturity, as presented in Figure 9, information may be derived on the seasons of growth and reproduction of *Sagitta elegans* on Georges Bank. In the cruise of September 1939, the immature individuals were somewhat more numerous than either of the other stages, but both Stages II and III were well represented. The latter stages were much smaller in size than the corresponding groups taken during the spring months. The modal length of the mature Sagitta was only 16 mm. in September as compared to 23 mm. in the following March. In the January cruise Stages I and II were encountered in about equal numbers, but very few mature specimens were present. By March and April the majority of individuals had matured to the Stage III condition, and remnants of these animals were still found in diminishing numbers (and in smaller sizes) in the May and early

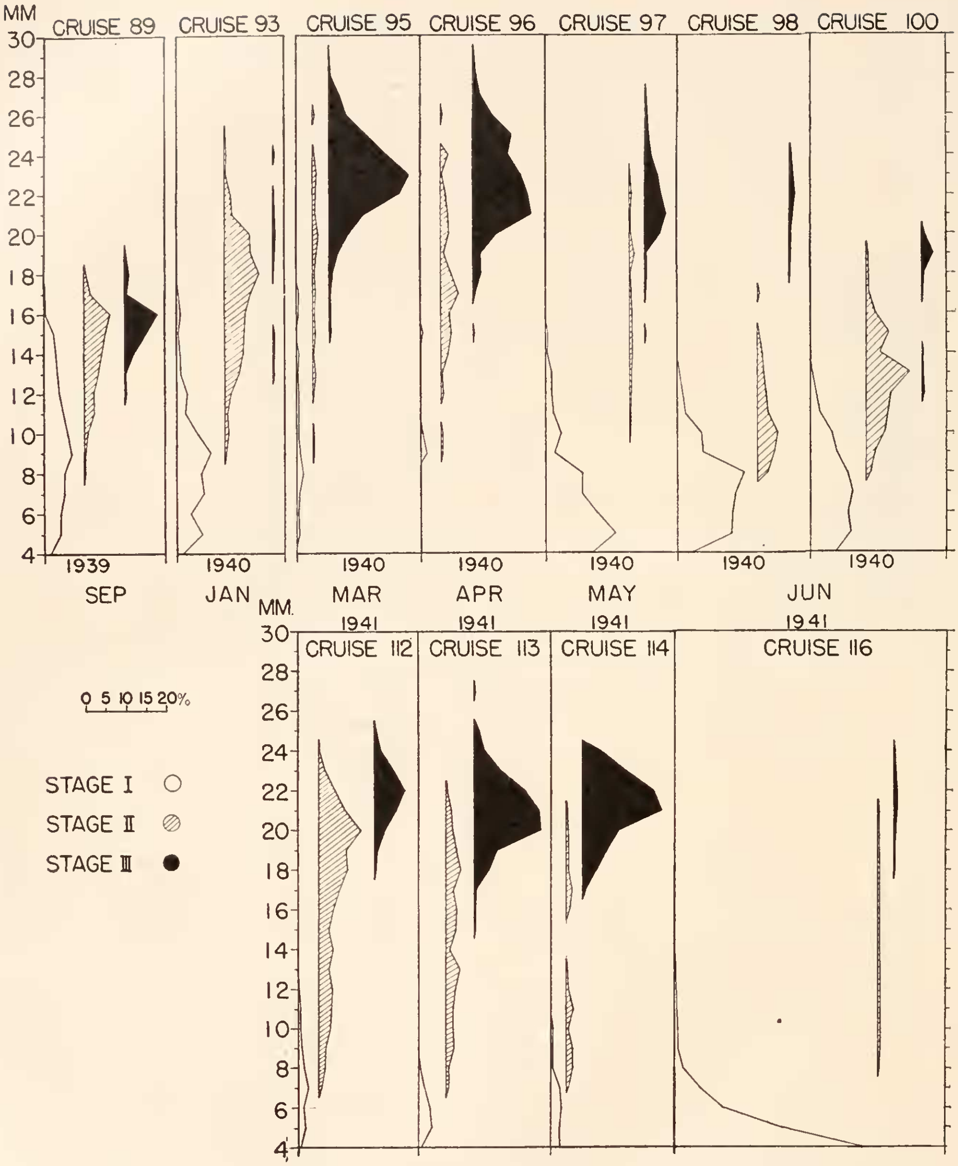

FIGURE 9. Stages of maturity and length frequency distribution for all cruises. Average values for *S. elegans* for all hauls in each cruise. Horizontal scale gives the percentage at each length, subdivided into the stages of maturity as indicated by the shading. Stage I—Immature, Stage II—Intermediate, Stage III—Mature.

June cruises. In May, however, the bulk of the catch consisted of immature specimens, and in the June cruises Stage I was also relatively the most abundant. Stage II was very scarce in May but appeared in increasing numbers (and in increasing sizes) in June. It is clear that this period of relative abundance of immature animals corresponds to the time of great increase in the actual numbers of smaller sizes which was noted in the previous section.

The striking difference observed in the lengths of the mature Sagitta at various seasons of the year is correlated in a general way with temperature. The shortest modal length for Stage III (16 mm.) occurred in September when the temperature of the water in the Mixed Area surpassed 16° C., the highest for the year, and the greatest modal length (23 mm.) was observed in March when the temperature reached a minimum of about 2.5° C. (Table II). As temperature increased through June, the mature sagittae became shorter again. Russell (1932) reported similarly that an inverse relationship existed between the length of the mature *Sagitta elegans* and the temperature of the water in the Plymouth Area, and the same tendency was observed in the Irish Sea by Pierce (1941). The maximum temperature recorded by Russell was about the same as in the present investigation, but the average length of his Stage III animals was only about 10 mm. On the other hand, the minimum temperature off Plymouth did not fall below 8° C. and the average length of the adult Sagitta was about 12 mm. in February, about 16 mm. in April to May 1931, and about 20 mm. in May 1930. No animals of length greater than 22 mm. were taken by Russell, whereas specimens as long as 30 mm. were encountered on Georges Bank. Our observations therefore agree with Russell's in revealing an inverse relation between temperature and body length, but the actual values are quite different. We have no information at present as to the mechanisms which underlie these relationships.

The changes in the Sagitta population during the spring of 1941 as revealed by the four corresponding cruises of that year, agree in general with those of the previous spring. There is, however, consistent indication that growth and reproduction were delayed in 1941 (Figure 9, bottom), although no important difference in the temperature of the Mixed Area water occurred for the corresponding months (Table II). In March 1941, there were relatively many more Stage II animals and many fewer Stage III individuals than in March 1940. The mature Sagitta dominated the scene in April 1941 and persisted in much higher relative abundance in May of that year than had been the case in 1940. At the same time it is to be noted that no important increase in Stage I is indicated in May 1941, in marked contrast to the previous year. Nevertheless, by early June 1941 (Cruise 116) small-sized Stage I animals appeared in very great numbers both relatively and absolutely. Stage III was reduced to a small remnant at this time, and there was no sign of an increase in the numerical strength of Stage II as had occurred in the previous June. It may therefore be concluded that in 1941 both the appearance of mature adults and the production of the large spring crop of young took place about a month later than in 1940.

An attempt may be made from the foregoing information to ascertain the annual cycle of growth and reproduction of *Sagitta elegans* on Georges Bank, but it is obvious that the gaps in the record during months in which no data could be obtained prevent final conclusions from being reached. It seems almost certain, however, that the chief period of reproduction centers in April or May because of the very high proportion of mature adults in those months, and the appearance subsequently of very large numbers of small, immature individuals. The adults which produced these animals apparently die off in June and the new crop of Sagitta matures during the summer to form a distinct generation of adults. This supposition is strongly supported by the fact that the Stage III animals found in September were of an entirely different size from those which had been prevalent in the spring. The graph (Fig. 9) suggests that the spring crop of young animals begins developing into Stage II in June with the possible appearance of a few of the new small-sized adults. The Stage I animals present in September may represent either the end of the spring and summer spawning or the beginning of the reproductive activity of the new generation of small adults. By January practically all of these small Stage III animals have disappeared and the immature individuals present are presumably their progeny. It seems safe to assume that the latter then slowly mature to produce the relatively large group of adults found in March and April, thus completing the cycle.

On the basis of the foregoing reasoning we may tentatively conclude that on Georges Bank *Sagitta elegans* undergoes one major period of reproduction during the spring months and that a distinct second generation is produced sometime in the late summer or autumn. It must be borne in mind, however, that during July and August and in the period between September and January, when no observations were made, another complete generation could have been formed. Russell (1932) believes that *Sagitta elegans* may complete a generation in as little as 43 days during the warmer months; and he has interpreted his data from the Plymouth Area as indicating that this species produces four or five generations during the course of the year. Pierce (1941), however, concludes that in the Irish Sea there is but one chief spawning period for *S. elegans* annually, extending from January through May. Our present data definitely indicate the existence of one major and one minor generation of this species in the Georges Bank area, but do not justify as yet any assumption that further generations occurred during the year.

Discussion

Information derived from the foregoing analyses of the distribution, growth, and reproduction of *Sagitta elegans* may now be examined as a contribution to the ecology of this species on Georges Bank particularly with reference to the currents of the region. Our previous knowledge of the occurrence of *S. elegans* off the New England coast has been summarized by Redfield and Beale (1940) in relation to their own studies of the sagittae in the Gulf of Maine. Although no special study of Georges Bank was undertaken by these authors, occasional stations on the Bank were occupied in the course of their survey, and at these stations large numbers of *S. elegans* were almost always encountered. These rich hauls contrasted sharply with the situation in the central area of the Gulf of Maine where the species was very scarce at practically every station. The explanation offered by Redfield and Beale is that water barren in respect to *Sagitta elegans* enters the Gulf each year and circulates through the central area so rapidly that sufficient time does not exist for large populations of this species to build up, even though the ecological conditions may be favorable in other respects. On Georges Bank, in contrast, these authors suggest that the water mass is sufficiently permanent to allow sagittae to accumulate and to further augment their number through effective reproduction.

The present investigation, based as it is on a much larger number of hauls on Georges Bank itself, not only tends to confirm the general suggestions of Redfield and Beale, but also provides strong evidence on the degree of permanence of the bank water. On the other hand, scrutiny of all the present data indicates that ecological factors other than simple transportation and accumulation play important roles in determining the distribution and abundance of the plankton. Redfield and Beale themselves point out that the central area of the Gulf of Maine supports a rich endemic population of Crustacea in spite of the fact that

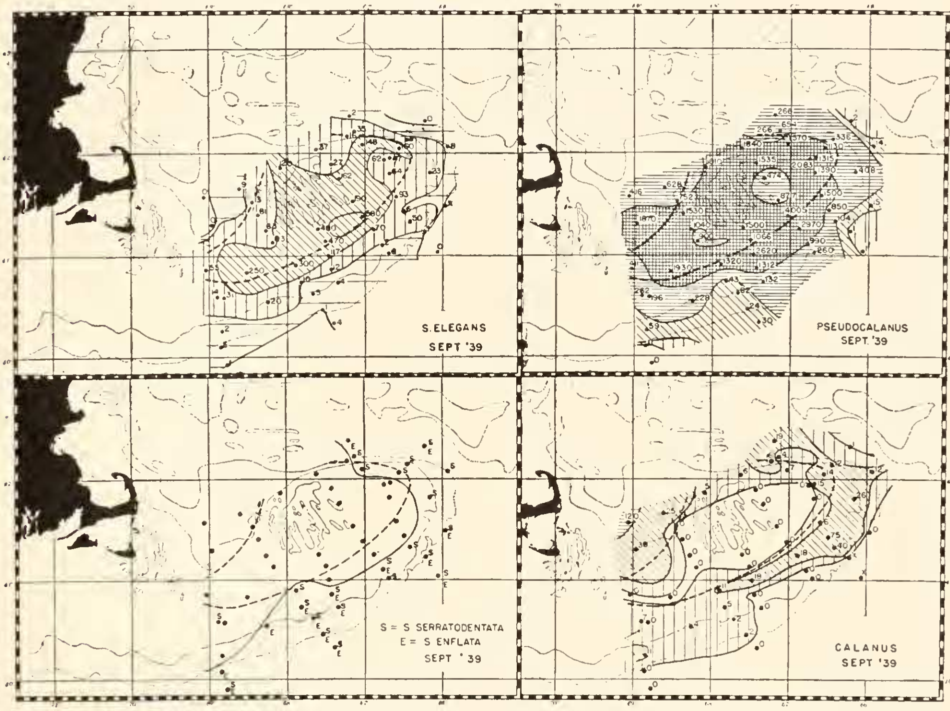

FIGURE 10. Comparison of the horizontal distribution of certain species of plankton in September 1939 (cruise 89). Distribution of *Sagitta elegans* is compared with that of *S. serratodentata*, *S. enflata*, *Pseudocalanus minutus*, and *Calanus finmarchicus*. Values shown are average numbers per cubic meter (per 10 cubic meters for *S. elegans*) for the whole water column for all stages of each species. Plankton Sampler hauls. Occurrence records for *S. serratodentata* and *S. elegans* are from the 75 cm. silk net hauls. The boundary of the Mixed Area is indicated by the heavy broken line. The symbol "X" represents a value of less than one individual per unit volume.

these animals are presumably subject to the same dislocating action of the currents as was invoked to explain the scarcity of *S. elegans* in that area.

The agreement of the distribution of *S. elegans* and of certain other species of plankton with the disposition of the water masses on Georges Bank during the present survey is well illustrated by the comparison for the cruise of September 1939, presented in Figure 10. Allusion has been made above to the close conformity of the main abundance of *Sagitta elegans* to the limits of the Mixed Area for that period. Two other species of *Sagitta* appeared during the September cruise in sufficient abundance to permit significant analysis of distribution to be made, although numbers were so small that presence or absence alone has been indicated in the chart of their occurrence (Figure 10, lower left). It is seen that the distribution of *S. serratodentata* and *S. enflata* was confined to the southern and eastern margins of the Bank in distinct contrast to *S. elegans*. A remarkably close agreement is observed between the line limiting the occurrence of the former and the margin of the Mixed Area. *S. serratodentata* occurred farther up on the Bank than did *S. enflata* but neither had been carried into the Mixed Area at more than one or two points. This fact shows that a very small amount of water, if any, was entering the Mixed Area from the south or the east at the time of this cruise.

It is of value to compare this striking case of the separation of two morphologically similar species by the hydrographical condition on the Bank with an equally clear-cut reciprocity in the distribution of two copepods, *Pseudocalanus minutus* and *Calanus finmarchicus* (Figure 10, upper right and lower right). Pseudocalanus occurred at all stations on the Bank during this cruise in very large numbers except along the southern and northeastern margins, but concentrations of over 1000 individuals per cubic meter were limited to the central region and to the north central margin, this zone of abundance corresponding closely to the Mixed Area.

In the case of Calanus, on the other hand, no specimens whatsoever were taken in the central portion of the Bank and very low counts were obtained for this species at every station within the Mixed Area (Fig. 10). Similarly small catches of Calanus were made along the extreme southern margin of the Bank and to the northeast, but considerable numbers were taken at the stations to the north and west toward the Gulf of Maine, and in the zone between the Mixed Area and the southern margin of the Bank. The tongue of water, rich in Calanus, which appears extending across the eastern end of the Bank and curving south and then west, is a clear indication that at the time of this cruise a current carrying Calanus from the Gulf of Maine was flowing around the margin of the Mixed Area and forming a wedge between it and the water masses to the south. At the same time mixed water, barren in respect to Calanus, from the central eddy of the Mixed Area appears to have been draining off to the west down the middle of the Bank. *Calanus finmarchicus* therefore appears to be a species which can endure neither the homogeneous water of the Mixed Area nor the warm, saline conditions to the south, but which thrives in the water of the Gulf of Maine. Thus Calanus is similar to *S. serratodentata* and *S. enflata* in being sharply excluded from the Mixed Area of Georges Bank, whereas Pseudocalanus and *S. elegans* are chiefly abundant within it.

Although one could argue that even if *S. serratodentata* and *S. enflata* found their way on to Georges Bank, they could not survive there because of lower temperatures and salinities, it is impossible to invoke these factors as preventing the occurrence of *Calanus finmarchicus* in the central part of the Bank. As we have seen, the water of the Mixed Area is chiefly derived from the Gulf of Maine where Calanus is abundant, and the temperature and salinity values of this water are generally intermediate between those of the upper and lower strata of the Gulf. Some other factor must be found which could prevent the repro-